

### 13.—Temperature Tolerance of the Chiton *Clavarizona hirtosa* (Blainville)

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Manuscript accepted—1st January, 1958.

The range of temperature within an individual chiton *Clavarizona hirtosa* is shown to be greater than the difference between the mean temperature of the chiton and that of the wet substrate. Experiments show there is no temperature control mechanism. The thermal death point was 43°C, both in sea water and in air, when the temperature was raised at 1°C per 5 min. The animals are shown to be more tolerant of sustained high temperatures in air than in sea-water. The lethal temperature is greater (by approx. 10°C) than temperatures occurring naturally in the chiton's habitat.

A comparison is made between two chiton populations. The effect of desiccation in relation to temperature is noted. The results are compared with similar experiments carried out in England, Bermuda and South Africa.

#### Introduction

Investigations on littoral ecology on the West Australian coast, undertaken by various people associated with the Department of Zoology, University of W.A., have posed questions concerning the temperature ranges tolerated by littoral molluscs. For the present investigations the chiton *Clavarizona hirtosa* (Blainville) was selected (a) because of its abundance, (b) because preliminary experiments showed that it tolerated the insertion of a thermocouple, and (c) because there has been little previous work of this nature upon chitons.

Only one reference to temperature effects on a chiton, Arey and Crozier (1919) and one to desiccation of a chiton, F. G. C. Evans (1951) have been found. These are discussed later.

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R. G. Evans (1948) summarises previous work on temperature tolerance of molluscs and points out that the "heat-light-desiccation" complex is probably the most critical of local climatic factors. Heilbrunn (1943) states, "Practically all animals and plants are killed at moderate temperatures which are usually only a few degrees above those at which they are accustomed to live normally. Indeed not infrequently heat death occurs in the normal environment." Broekhuysen (1940), although noting that thermal death points of several gastropod species (measured in the laboratory) were never reached in natural conditions, nevertheless recorded that six South African gastropods showed a direct correlation between thermal death-point and the height of zonation of the particular species on the shore. It was also reported by Gowanloch and Hayes (1926) that within one species, animals collected from different tidal levels showed a lethal temperature gradation.

#### Ecology of *Clavarizona*

The west coast limestone reefs show typically a "visor", an intertidal undercut at approximately mean sea level and a reef platform at about M.L.W. which terminates abruptly at its seaward edge, often with a narrow, raised rim (Fig. 1). An account of the geological structure of these reefs is given by Fairbridge (1950) and tidal data for the region has been analysed by Bennett (1939) and more recently by Hodgkin and Di Lollo (1958).

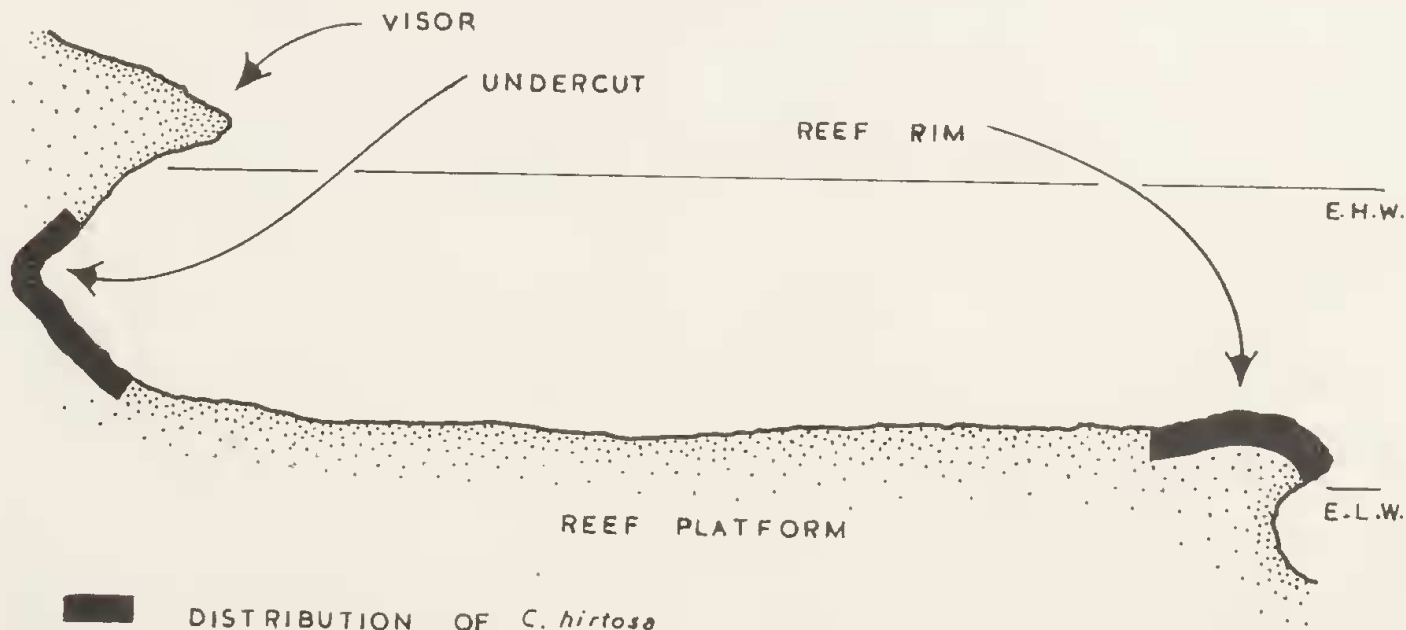


Fig. 1.—Diagram of section through typical limestone reef platform. Vertical scale greatly exaggerated.

Resting chitons are found near the reef rim and on the rock surface in the undercut between tide levels. Where there is no reef platform there is only a single zone of *C. hirtosa* in the undercut.

Although chitons in an undercut may be out of the water for several hours each day, and with low tides and calm weather may be fully exposed to air for the greater part of the day, individuals are generally protected from the full effects of the sun for much of the time by the rock visor.

Individuals situated near the reef rim are rarely exposed to temperature conditions other than those of sea water since, in general, surf conditions are such that even at low tide the reef edge is awash. The reef rim is exposed only when a low sea level, a small tidal range and calm weather coincide. Local tidal and climatic peculiarities are such that the possibilities of these factors summing in the hot and sunny period of a summer day are rare.

*Clavarizona hirtosa* has been recorded (Hull 1922) on the West Australian coast from Pt. Cloates (22°35' S, 113°50' E) to Eyre (32°15' S, 126°15' E), ranging from tropical to warm temperate climates. The mean maximum air temperature at Carnarvon (25°0' S, 113°50' E) in February is 31.5°C and the mean minimum air temperature at Albany (35°0' S, 118°0' E) in July is 7.5°C; extreme summer maximum air temperatures above 40.0°C have been recorded from Carnarvon and Perth (31°55' S, 115°50' E) and extreme winter minimum air temperatures at Albany approach freezing point.† Water temperatures in this area vary from a summer monthly mean of 24°C off Shark Bay to a winter monthly mean of 14°C near Albany (Royal Netherlands Meteorological Institute, 1949).

Extreme temperature readings, taken within a few yards of the source of specimens for present experiments, at Cottesloe Beach (near Perth) at various times from 1944 to 1954 are summarised in Table 1.

TABLE I

Location	Temp. ° C
rock surface in sun	up to 44.0
air shade	6.1 to 33.2
rock pools	7.6 to 34.6
sea at shoreward edge of reef flat	10.0 to 27.3
surf at outer reef edge	14.7 to 23.5

#### Methods and Results

Temperature observations on the chitons can be grouped under the main headings:

- (i) Temperature variations within one chiton.
- (ii) Field measurements in the normal habitat.
- (iii) Field measurements in an extreme habitat.
- (iv) Laboratory experiments on thermal death point in sea water.
- (v) Laboratory experiments on thermal death point out of sea water.
- (vi) Effects of desiccation.
- (vii) Behaviour observations in relation to temperature.

† Data from the Perth Office of the Commonwealth Bureau of Meteorology.

Field measurements were carried out at Rottneest Island (32°S, 115°25' E) during November 1951 and at Cottesloe Beach in December 1954 and January 1955, and laboratory observations were made during the summer periods 1951-52 and 1954-55 on animals collected from Cottesloe Beach. Fresh specimens were brought in for each set of observations and were kept in laboratory conditions for some hours prior to commencing any heating experiments. In all laboratory experiments a set of control chitons were treated similarly to the experimental animals except that they were not heated.

All temperatures were recorded with a Cambridge skin temperature thermocouple, and sea water and air temperatures were checked with a mercury thermometer. Humidities were recorded using an Edney torsion hygrometer and checked where possible with a wet and dry bulb instrument.

#### (i) Temperature variation within one chiton

Animals were taken from sea water at 21.2°C and placed on a smooth glass surface in air at 24.9°C and relative humidity, 54% in the laboratory. After five minutes to allow the chiton to settle readings were taken inserting the thermocouple in different parts of the body. Handling the animals was avoided as far as possible and when it was necessary to shift the animal to insert the instrument (e.g. readings in the foot) the animal was replaced and held in contact with the glass plate by a plastic rod. Readings were taken with chitons on a wet surface and on a slightly warmed dry surface. The results are summarised in Table II, and show a variation within one animal of from 1.0°C to 2.6°C.

TABLE II

Temperatures of various parts of individual chitons (measured in °C)\*

Chiton	A	B	C	D	E
AIR	24.9	24.9	24.9	24.9	24.9
SURFACE	29.6	28.9	22.8	22.8	22.8
girdle	25.9	25.8	21.8	22.6	22.8
gills	25.4	27.4	23.0	23.5	22.4
foot	26.7	28.3	24.1	22.5	22.0
mouth	25.8	27.6	21.5	22.8	22.8
anus	25.3	...	22.9	22.9	23.5
visceral mass	26.1	27.7	23.3	22.8	23.3
between foot and glass	...	...	...	21.9	22.6

\* Animals A and B on a dry plate, C, D and E on a wet plate.

#### (ii) Field measurements in the normal habitat

Observations were made on chitons (*in situ*) in the undercut at various points along approximately one half mile of shore line at Rottneest Island, reading in each case air, rock surface and animal temperature. The thermocouple needle was inserted through a small hole pierced in the girdle of the animal and was pushed in far enough to be in contact with the lateral wall of the visceral mass. The chitons showed no obvious ill effects from this treatment and the same animals could be used repeatedly without them detaching from the rock surface.

One hundred and twenty-four readings were taken over a range of rock temperatures from 16.2° to 34.0°C. Experimental animals were

selected at random except that for the higher temperature group it was necessary to choose animals continuously in the sun.

The results are expressed graphically in Fig. 2. In some cases the range of animal temperatures associated with a particular rock temperature is wide, and this can be explained in part by the field notes on recent shading or wetting of individuals although often it was not possible to record quantitatively these microclimate variations.

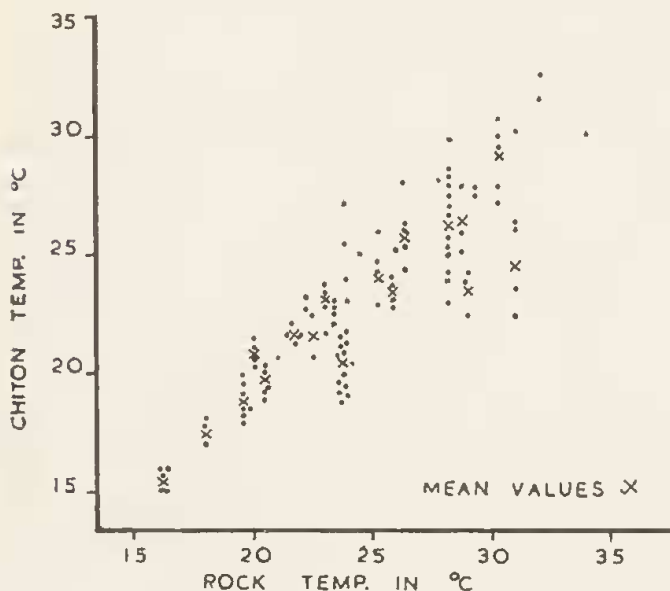


Fig. 2.—Temperatures of chitons (in the field) plotted against rock temperatures.

The geometric means plotted show a correlation between rock temperature and chiton temperature within the range of temperature variation of one animal, except in the groups of recently wet or shaded specimens where the mean animal temperature (24.5°C) was 6.5°C below the rock temperature.

(iii) *Field measurements in an extreme habitat*

Several readings were made during one day on small groups of animals in sunny and exposed conditions not typical of the usual situation in the undercut of *C. hirtosa*. The temperatures of individual animals followed the changes in rock temperature closely. Once covered by the incoming tide both the rock surface and the chitons returned to the water temperature. One set of these readings is shown in detail in Table III.

TABLE III

*Variation of temperature of a group of chitons*

Time	Air T. °C	Rock T. °C	Sea T. °C	Chitons T. °C				
				A	B	C	D	E
0645	18.3	18.0	....	17.7	17.8	17.3	17.5	17.6
0935	23.8	23.8	....	20.7	20.5	21.2	21.6	21.6
1240	26.8	25.2	....	24.2	23.0	26.0	24.7	24.2
1500	23.2	30.3	....	30.0	30.8	28.0	29.8	27.2
1725	23.3	21.6	21.6	21.5	21.7	21.4	21.7	21.7

The close correlation between chiton temperature and rock temperature, the rate of change of these two temperatures (Table III), also the temperature lowering shown by some animals (Fig. 2), suggested that there was some temperature control mechanism. The temperature changes of a group of chitons including living and dead animals and dead animals kept wet were measured. It was assumed that this would show whether or not living *Clavarizona* can control body temperature.

The chitons were taken from the undercut at Cottesloe Beach and reattached to the rock on the upper surface of the visor (about two feet vertically above their original position) in sunshine. The dead animals were killed by immersion in hot (70°C) sea water for ten minutes and were fixed to the rock surface with clear plastic adhesive tape. Readings were taken over a period of ninety minutes and the "dead-wet" chitons were damped after each reading with sea water at 23.3°C (the water and rock temperature from which all animals were originally taken). The wind velocity one foot above the rock surface where the chitons were attached varied during the experiment from 5 to 10 miles per hour. The results are shown graphically in Fig. 3.

The similarity of the readings from living and dead animals shows clearly the lack of any temperature regulating mechanism in *C. hirtosa*, while the lowered temperatures recorded from the dead-wet specimens show the physical effect of evaporation.

The living chitons responded normally when returned to sea water.

(iv) *Laboratory experiments on thermal death point in sea water*

Heilbrunn (1943) points out that the lack of details regarding rate of heating has marred otherwise useful records of heat death. In order to make these results comparable with other work (Gowanloch and Hayes (1926), Broekhuysen (1940) and R. G. Evans (1948) ) a standard rate of 1°C per 5 minutes was adopted. R. G. Evans (1948) states that "this is sufficiently slow to make any lag between the body temperature and that of the surrounding water small enough to be neglected."

Additional experiments were carried out with the rate of heating slowed down to 1°C per 15 minutes which was considered to be more nearly the rate met with in nature and with the rate speeded up to 1°C per minute to note any variation in reaction to different rates of heating. In each case the chitons were kept at the final temperature for from three to five minutes.

Direct transfer from seawater at 26°C to seawater at various temperatures up to 45°C (as in the experiments of Arey and Crozier (1919) ) was considered unsuitable.

The observations were made on animals heated in dishes approximately 15 cm in diameter and holding 500 ml of seawater. The number of animals per bowl was restricted to five as it was considered that this should provide a suitable amount of available oxygen and space for the chitons. These bowls were heated several at a

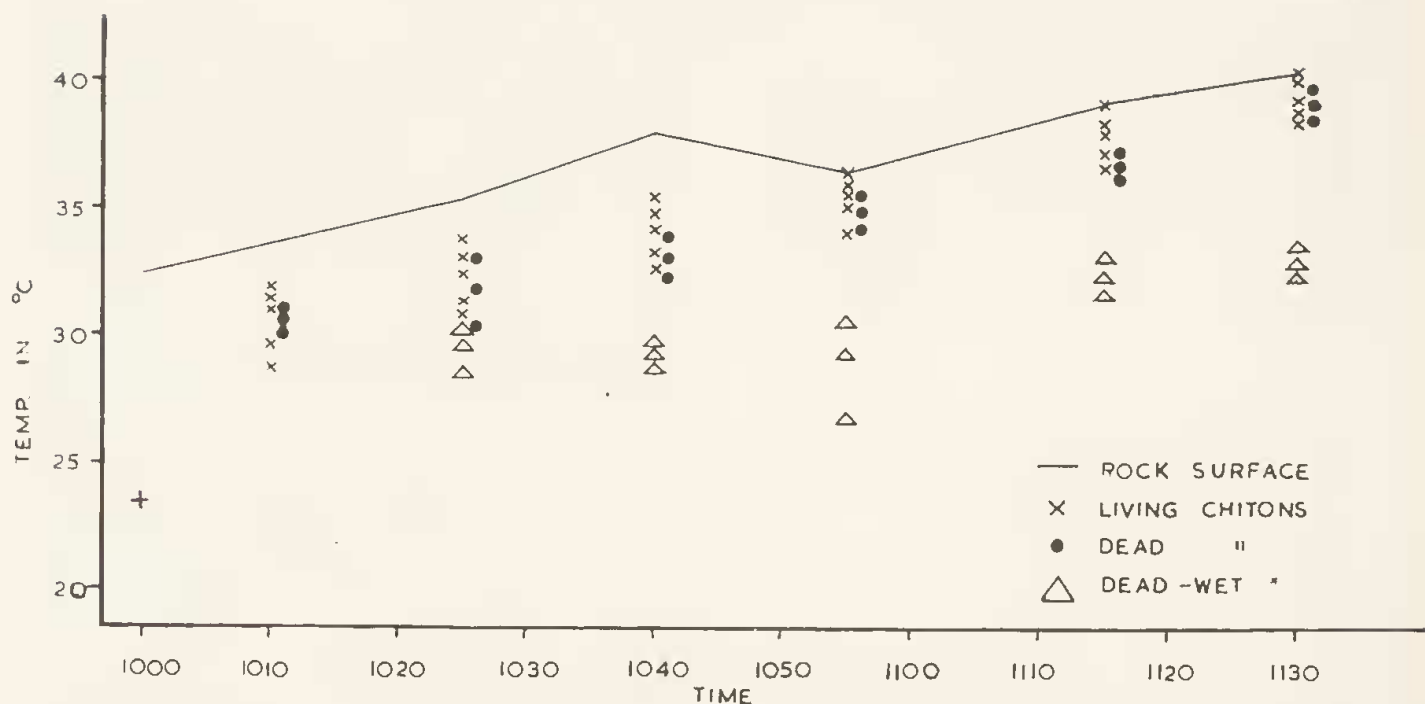


Fig. 3.—Temperatures of living and dead chitons (in the field).

time in a large water bath and temperatures were read in the bowls, not in the water bath. Aeration throughout the heating period and after was effected by vigorous stirring. No depletion of water volume was noted during any of the experiments.

After subjection to the particular temperature desired the animals were removed from the water bath (remaining in the warmed sea water) and allowed to cool to air temperature. When the heated water had returned to room temperature it was replaced by fresh sea water; this, depending on the rate of cooling, was done from three to six hours after the conclusion of the heating period. Twenty four hours were allowed for the chitons to revive and during that time the water was renewed several times.

The chitons were then tested for response to stimulation, the foot being pricked by a needle, and animals showing no response were considered dead. The lethal temperature was taken as that which killed fifty per cent of the animals tested.

TABLE IV

*Lethal temperature of C. hirtosa in sea water*

Final T. °C	Rate of Heating					
	1°C/5 min.		1°C/15 min.		1°C/1 min.	
	No. of animals heated	No. surviving	No. of animals heated	No. surviving	No. of animals heated	No. surviving
38	7	7	5	5	5	5
40	7	7	10	4	5	5
41	9	9	7	1	5	3
42	11	10	5	0	5	1
43	23	8	5	0	5	0
44	10	0				

The lethal temperature in seawater of *C. hirtosa* was determined as 43°C for a 1°C per 5 minutes rate of heating, 42°C for a 1°C per

minute rate and 40°C when heated at 1°C per 15 minutes. Table IV summarises the details of these experiments.

A comparable set of heating experiments, at 1°C per 5 minutes, was carried out using animals taken from the reef rim and it was shown that the lethal temperature for this group of chitons was 41°C. (Table V).

TABLE V

*Lethal temperature in sea water of C. hirtosa from the reef rim*  
Rate of heating 1° C per 5 min.

Final T. °C	No. heated	No. surviving
38	5	5
39	5	5
40	10	6
41	10	4
42	5	0
43	5	0

In order to relate thermal death to length of exposure to particular temperatures, as suggested by Heilbrunn (1943) groups of chitons were heated (as described above) at a rate of 1°C per 5 minutes to final temperatures from 38° to 44°C and held at these temperatures for varying lengths of time. (Table VI). It will be seen from the table that although only a few animals survived exposure to 43°C for 5 minutes, at 41°C or less death was produced only by prolonged exposure.

The experiment at 38°C was discontinued after two and one half hours.

(v) *Laboratory experiments on thermal death point out of sea water*

Experiments on the effects of temperature on *Clavariopsis* out of sea water were carried out with animals placed on a dried enamel surface in the laboratory. Both wet and dry bulb air temperature readings were taken and the humidity in the proximity of the testing plate was checked frequently with the Edney instrument. The test plate was heated over a water bath.

TABLE VI

*Tolerance of C. hirtosa to prolonged heating in seawater*

Temp. ° C	Time (in minutes after reaching T.)												
	5	10	15	20	25	30	45	60	75	90	120	150	
44	10	0											
43	23	8											
42	11	10	5	0									
41				2									
40				12	9	12	7	12	6	12	5	5	5
38				7	7					10	8	12	6
										10	10	10	3
											10	8	10
												10	9

In each column—the first figure = no. of chitons heated, the second figure = no. of chitons surviving. Laboratory air temperature varied between 22.7° C and 29.4° C.

In order to check the time required for chitons to assume the temperature of the surface a group of five animals was taken from sea water at 23.1°C, placed on a dry surface at approximately 40°C, and kept there until the animal temperatures were stable over a period of ten minutes.

The frequent readings necessary made it impossible to check each animal as often as would be desirable but the graph of the results (Fig. 4) shows that the temperatures of different chitons at any one time were reasonably similar.

Within ten minutes the specimens had reached stable temperatures varying from 38.6° to 40.7°C and maintained these for a further ten minutes. The slight variations in the recorded surface temperatures were within the range of variation in a single chiton.

In order to compare the death point due to heat in air with that previously recorded in sea water groups of *C. hirtosa* were heated on a dry plate. The procedure used was the same as in the sea water experiments, the rate of heating being approximately 1°C per 5 minutes. As small variations in the temperature of the enamel surface were common and the lag between surface and animal temperatures was not constant,

the final temperatures read were those of the chitons and not of the plate. The interval between final temperatures was limited to 2°C.

The thermal death point was 42 to 44°C. The detailed results are listed in Table VII.

TABLE VII

*Lethal temperature of C. hirtosa out of sea water*

Temp. ° C	No. of animals heated	No. of animals surviving
30	3	3
35	3	3
38	5	5
40	6	5
42	20	12
44	10	2

Other animals were tested while attached to damp and dry slabs of limestone, taken from Cottesloe Beach, both in-doors and in a sheltered but sunny situation. The varying rates of evaporation from the rock surface and of temperature increase and changes in relative humidity made the results difficult to analyse and they are not recorded here. However it is worthy of note that those animals removed at 42°C or less revived, while those (six in number) submitted to higher temperatures did not.

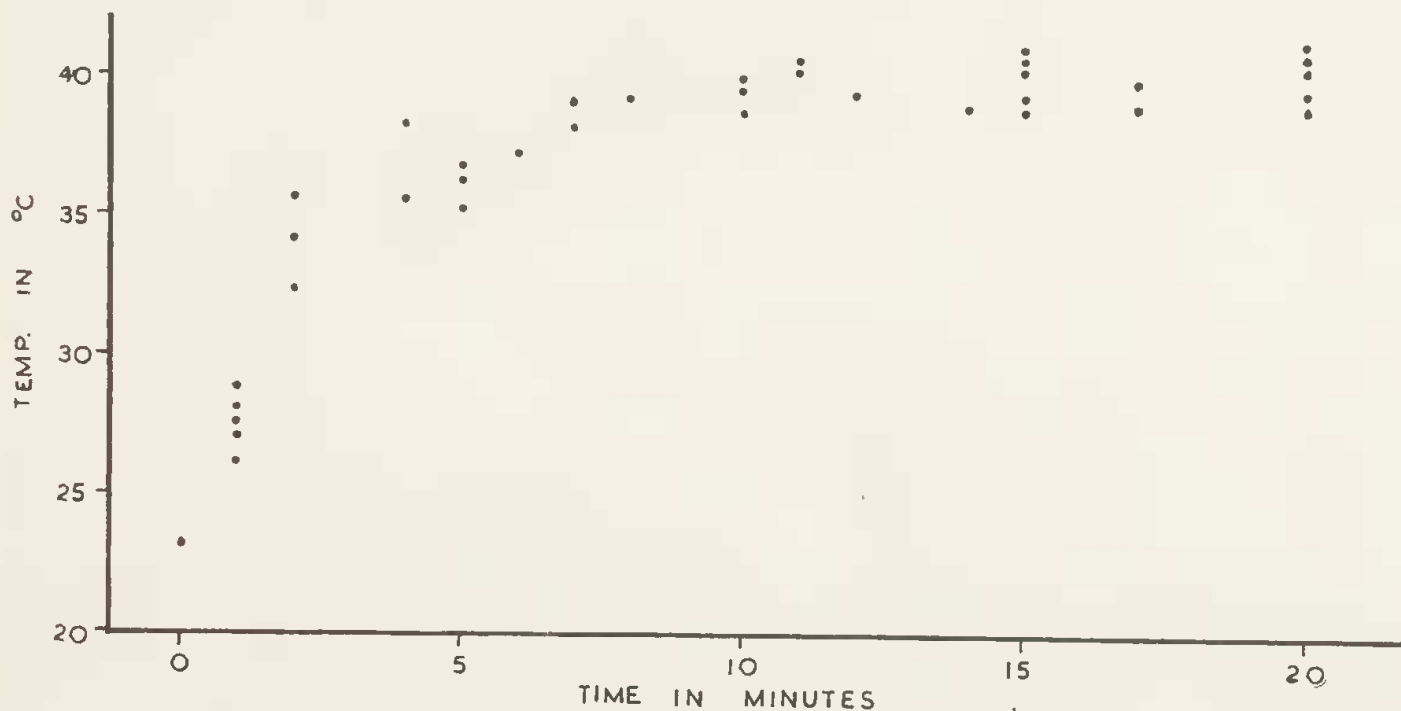


Fig. 4.—Time taken for chiton temperature to stabilise (in the laboratory).

A group of chitons from the reef edge was heated on the test plate in the laboratory. Four out of five animals survived exposure to 40°C for 5 minutes, but all chitons heated to 42°C died.

Groups of specimens were transferred from water to the test plate which had previously been warmed to 40°C, and were kept on the plate for varying periods. The length of time that the animals were kept at 40°C was noted from ten minutes after they were attached to the heating plate. In order to keep the chiton temperatures at 40°C ( $\pm 1.0^\circ\text{C}$ ) it was necessary to vary the plate temperature (up to 43.5°C at one period).

The water temperature, from which the chitons were taken and to which they were returned, was 21.8°C, air temperature 23.6°C and the relative humidity 62%.

The experiment was discontinued after ninety minutes (i.e. 80 minutes at 40°C) as it was considered that exposure for this period may cause death from desiccation (see section vi below). The results are inconclusive (Table VIII).

TABLE VIII  
Chitons in air, kept at 40°C

Time (after stabilisation)	No. heated	No. recovered
20 mins	5	5
50 mins	10	7
80 mins	5	4

(vi) Effects of desiccation

In the above experiments on chitons out of seawater, the possibility of death being due to the combined effects of heat and desiccation was appreciated but not considered. The experiments were repeated to measure water loss.

Individual chitons were dried with filter paper and weighed (this weight being taken as the standard weight) before heating. At intervals animals were removed from the heating plate, reweighed and returned to seawater. The water loss was calculated as a percentage of the standard weight.

Figs. 5 and 6 show the details of these experiments graphically.

The range of the results makes any definite correlation between either rate of heating or final temperature and loss of weight difficult. The rate of dehydration is greater at higher temperatures initially, but the curve of dehydration rate tends to flatten off after approximately 60 minutes heating. The animals at 40°C for the total period of time lost a greater amount of water than those heated gradually (the mean values for 60 minutes being 16% and 10% respectively). Of animals showing a 15% or greater water loss, 7 out of 10 failed to recover. The lowest percentage water loss at which death occurred was 9%.

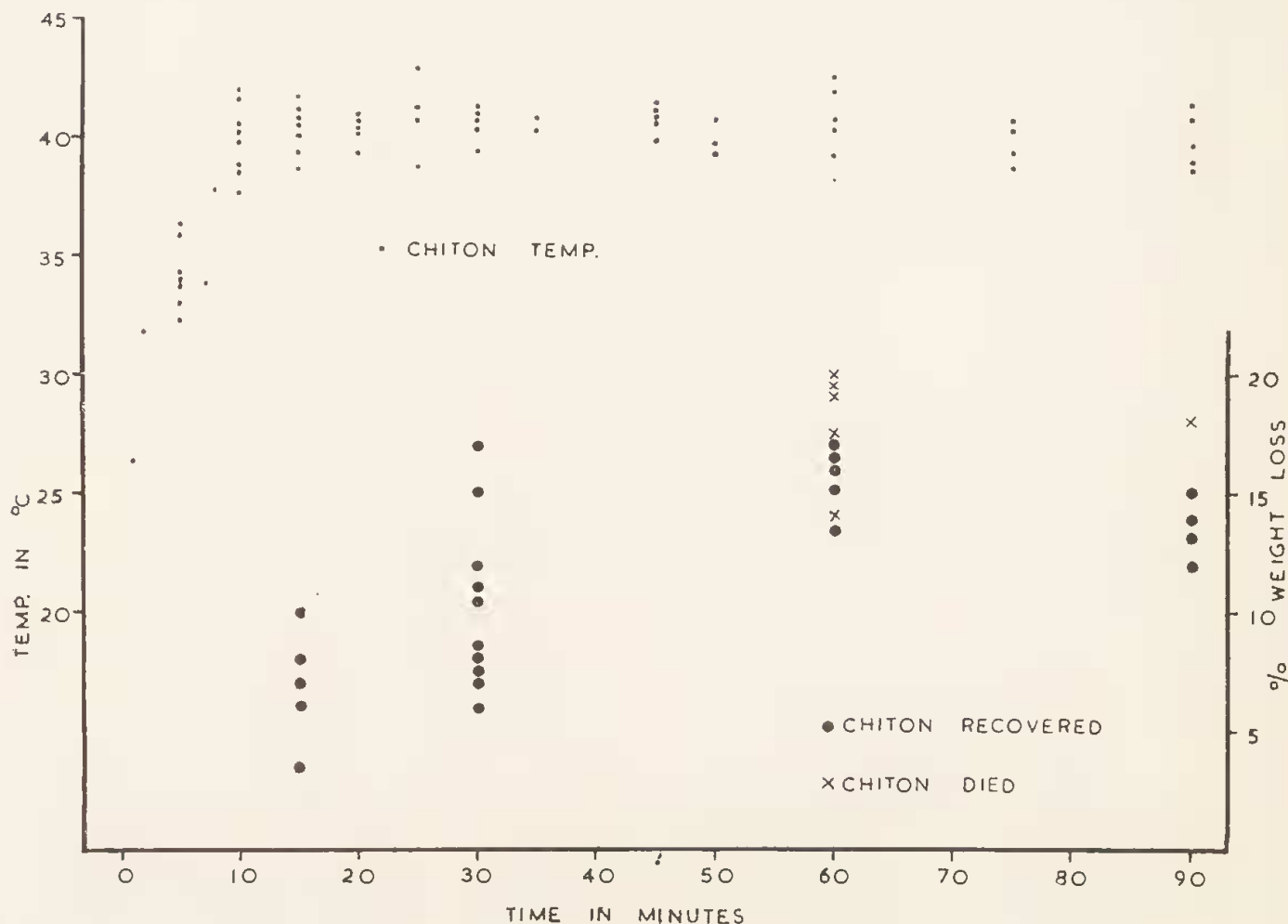


Fig. 5.—Percentage weight loss by chitons kept at 40°C.

(vii) Behaviour observations in relation to temperature

Throughout the experiments notes on the behaviour of the chitons were taken.

At temperatures near 30°C many of the animals being heated in sea water became more active and as well as moving quite rapidly up the sides of the bowls, tended to rear up in a "rampant position" remaining attached to the glass surface by only a small area of the foot. In the low thirties active crawling usually ceased and some animals raised the girdle. From 33°C upwards the ability to remain attached to the glass surface appeared to be lost, though in some cases the test animals remained fixed to the side of the bowl, by mucus, even after reaching the lethal temperature. At approximately 34°C all activity stopped and in general the chitons remained quiescent at higher temperatures.

No major difference in the reaction to particular rates of heating was noted though at the slower rate (1°C per 15 minutes) no chitons detached from the surface below 36°C.

Specimens heated in air on the test plates in the laboratory showed no special reactions. Chitons which were only partially in contact with the surface showed the same rate of temperature change as those that were firmly fixed.

Some animals heated on limestone detached at approximately 36°C, but detached animals revived as readily as those at the same temperature which had to be removed forcibly. In this experiment one chiton crawled to the shaded undersurface of the rock when the limestone temperature was 29.0°C and the animal's temperature 26.5°C.

No difference in behaviour was noted in chitons collected from the undercut and those taken from the reef rim.

Discussion

Writing on *Chiton tuberculatus*, from Bermuda (lat 32°N), Arey and Crozier (1919) state, "Temperatures of 44°C to 45°C are almost instantly fatal, although Chiton will survive for nearly two hours after sudden transference to a temperature of 40°C." These results are similar to those obtained with *Clavarizona hirtosa* i.e. 50% death at 43°C (5 minutes), no survivals at 44°C (5 minutes) and a 50% death after 75 minutes at 40°C. Thus similar heat death points have been recorded for two species of chitons from somewhat similar climatic regions.

It has been shown by Huntsman and Sparks (1924) that marine organisms have a degree of resistance to heat correlated with the temperature ranges the species experience in nature and Gowanloch and Hayes (1926) have demonstrated that animals of the same species from different tidal levels have different lethal temperatures (see also Broekhuysen (1940), in the Introduction). The results of these experiments with *C. hirtosa* conform to this pattern, individuals from the undercut having a higher lethal temperature (43°C in seawater) than those taken from the reef rim (41°C in seawater).

From the figures available (Table 1) and field observations, the difference between the maximum temperatures likely to be met by these two populations would be much greater than the difference between their thermal death points.

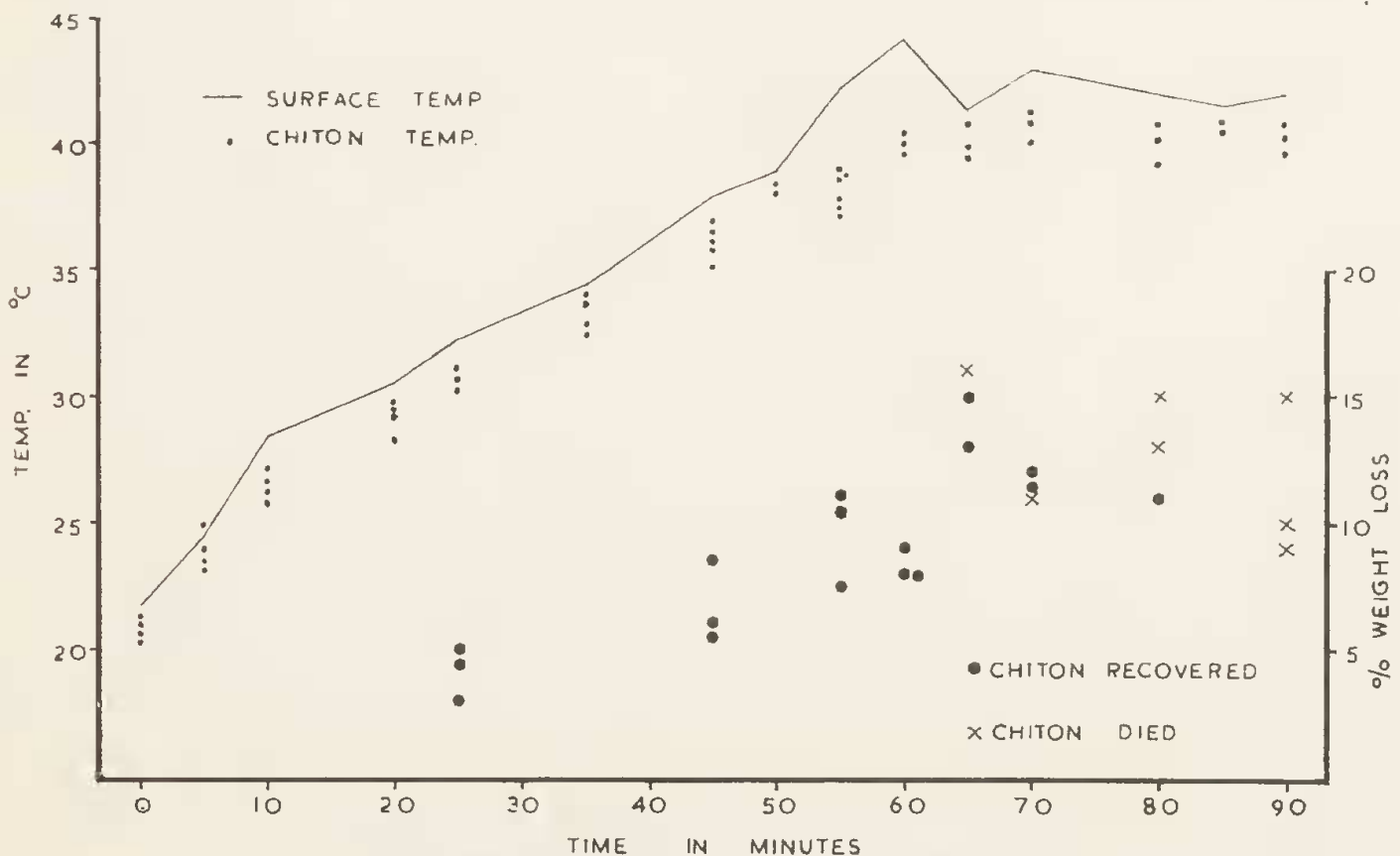


Fig. 6.—Percentage weight loss by chitons gradually heated to 40°C.

Heilbrunn (1943) states, "ordinarily dry heat does not kill as readily as wet heat." Although in the case of *C. hirtosa* there is no difference between the temperature producing death in water and in air this species is more tolerant of sustained high temperatures in air. Specimens kept at 40°C in air for a period of ninety minutes were much less affected than those treated similarly in sea water (only 3 out of 10 animals surviving in the latter instance).

Hogben and Kirk (1945) found that the slug *Arion ater* and to a lesser extent *Helix pomatia* behaved as a wet bulb thermometer, with the cooling effect of evaporation preventing the body temperature from rising to that of the surrounding medium, unless the air was fully saturated. The snail when withdrawn into the shell assumed a temperature considerably above that of the wet bulb and more nearly followed the dry bulb temperature. The slug, being shell-less was not able to control the loss of water by evaporation and remained at a lower body temperature even when the surrounding medium was at a temperature above the danger level for the animal.

*C. hirtosa* however is dependant on the temperature of the substrate and surrounding air temperature is only of importance in so far as it affects the rock (or other surface) temperature. The similarity of the reading obtained from living and dead chitons show clearly that there is no temperature reducing factor controlled by the animal, while the different temperatures recorded from the dead-wet specimens give some indication of the degree to which evaporation could lower body temperature if a mechanism for the control of temperature by evaporation did exist. However, it should be pointed out that in the experiment the whole dorsal surface including the shell was available for continued evaporation, whereas if evaporation was being used by the animal as a temperature control mechanism the surface would not be redamped periodically and that evaporation from the surface of soft tissues (e.g. mantle cavity and gills) would eventually result in complete desiccation.

Broekhuysen (1940) working with various intertidal molluscs in South Africa (where climatic conditions are similar to West Australia) found that "the minimum percentage of water loss at which death occurred" at 40°C was 10% for *Oxysteles variegata* (Anton) and 13% for *Thais dubia* (Krauss). These two species have vertical ranges comparable with *C. hirtosa*. He further showed that they were slightly more tolerant of desiccation at room temperature.

*Lepidochitona cinereus* (L) specimens kept in still dry air (over calcium chloride) at room temperature for seven hours by F. G. C. Evans (1951) showed a mean loss of weight of 12% and, of 14 animals tested, 2 were dead. After 22½ hours all the chitons had died and the average weight loss was 52%.

Although F. G. C. Evans' experiments were carried out at room temperature and Broekhuysen does not state the duration of his experiment the figures for minimum water loss causing death are similar to that obtained for the West Australian chiton (9% loss of weight after 90 minutes).

Direct comparison between the rate of desiccation of *Clavarizona* and Broekhuysen's molluscs is unreasonable as the South African species used were gastropods, presumably capable of controlling desiccation to some degree by closing the operculum. However the flattening of the rate of desiccation curve mentioned by Broekhuysen is paralleled in the case of the chiton although the rate is much more rapid. *C. hirtosa* specimens kept at 40°C for 90 minutes having lost 15% of body weight while an equivalent water loss from *Thais dubia* at room temperature took 20 hours.

The figures (for species with similar vertical distribution to *C. hirtosa*) listed by Broekhuysen (1940) as "temperature at which activity stopped" and by R. G. Evans for "inactive but responding to stimulation", vary from 32°C for *Littorina littorea* (L) to 37.2°C for *Oxysteles variegata* (Anton). These are similar to the 34°C cessation of activity of *Clavarizona*.

*Clavarizona* situated, as it is typically, in the undercut and at the reef edge would not normally be faced with temperatures approaching the lethal point, but extreme conditions of low tides in the hottest part of the day during the summer period certainly do produce rock temperature up to 44°C on the visor (see Fig. 1). The few chitons observed occurring naturally at this level tend to be situated in small crevices apparently making use of the meagre shade available, or in rock pools. Fig. 2 shows clearly the body temperature variation produced by factors of the microclimate.

The damp shaded conditions of the undercut would rarely produce extreme desiccation conditions but raising the chitons two feet vertically would in many cases place them in a position where low humidities occur frequently during the summer months and since they would remain exposed to the air for prolonged periods a water loss of 15% would be probable.

R. G. Evans (1948) comments, "From what is already known it appears probable that the effects of temperature acting as an isolated factor (i.e. pure temperature effects) are of subsidiary importance to the drying action of super-normal temperatures in controlling the upper limits of distribution of littoral plants and animals." Presumably this would only apply to chitons if they were detached from the rock surface.

The pure temperature effect necessary to kill *Clavarizona* is approximately 10°C above the temperatures recorded in the undercut in the field although higher temperatures may occur. It is in the undercut that the majority of the population occurs and this suggests that extremes of heat and desiccation that will kill *Clavarizona* are rarely experienced in this niche.

These experiments were done on animals from the middle of the geographic range of *Clavarizona* and it is probable that specimens from the northern extreme of the range may show effects of acclimatisation to the overall warmer conditions, although the extreme air temperatures recorded from Perth are similar to those recorded at Carnarvon (six degrees of latitude further north).



### Acknowledgments

The writer wishes to thank Professor H. Waring, Zoology Dept., University of Western Australia, for making available the accommodation and equipment which enabled these experiments to be carried out, and to acknowledge gratefully the assistance with field work given by various staff and student members of the Department. Thanks are due in particular to Dr. E. P. Hodgkin for considerable practical help and advice and to Mr. R. L. Kirk for advice on the use of the Cambridge skin temperature instrument which the Department made available.

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